

heavy-ion accelerator. Accumulation between the cycles of a small ring used to feed a large, high-energy machine could greatly increase the beam luminosity for high-energy experiments. □

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- Budker, G. I. *Proc. Int. Symp. on Electron and Positron Storage Rings* (eds Zyngier, H. & Cremieux-Alcan, E.) II-1 (Presses Univ. de France, Paris, 1967).
- Van der Meer, S. *CERN/ISR-PO/72-31* (CERN, Geneva, 1972).
- Möhl, D., Petrucci, G., Thorndahl, L. & Van der Meer, S. *Phys. Rep.* **58**, 73-119 (1980).
- Van der Meer, S. *Rev. mod. Phys.* **57**, 689-697 (1985).
- Budker, G. I. *et al. Partical Accelerators* **7**, 197-211 (1976).
- Bell, M., Chaney, J., Herr, H., Krienen, F. & Petrucci, G. *Nucl. Instrum. Meth.* **190**, 237-255 (1981).
- Ellison, T. *et al. IEEE Trans. Nucl. Sci.* **NS-30**, 2636-2638 (1983).
- Poth, H. *et al. Nucl. Instrum. Meth.* **A287**, 328-332 (1989).
- Steck, M. *et al. Nucl. Instrum. Meth.* **A287**, 324-327 (1989).
- Blasche, K. & Böhne, D. *Proc. 14th Int. Conf. High Energy Accelerators Chicago* (American Institute of Physics, New York, 1989).
- Derbenev, Ya. & Skrinsky, A. N. *Particle Accelerators* **8**, 1-20 (1977).
- Derbenev, Ya. & Skrinsky, A. N. *Particle Accelerators* **8**, 235-243 (1978).
- Ogino, T. & Ruggiero, A. G. *Particle Accelerators* **10**, 197-205 (1980).
- Bell, J. S. & Bell, M. *Particle Accelerators* **11**, 233-238 (1981).
- Sørensen, A. & Bonderup, E. *Nucl. Instrum. Meth.* **215**, 27-54 (1983).
- Budker, G. I. & Skrinsky, A. N. *Soviet Phys. Usp.* **21**, 277-296 (1978).
- Derbenev, Ya. & Skrinsky, A. N. *Phys. Rev. Vol. 3* (ed. Khalatnikov, I. M.) 165 (Harwood Academic, Chur, 1981).
- Cole, F. T. & Mills, F. E. *A. Rev. Nucl. Particle Sci.* **31**, 295-325 (1981).
- Skrinsky, A. N. & Parkhomchuk, V. V. *Soviet J. Particle Nucl.* **12**, 223-247 (1981).
- Poth, H. *Proc. CERN Accelerator School*, CERN 87-03, 534-569 (CERN, Geneva, 1987).
- Poth, H. *Phys. Rep.* (in the press).
- Poth, H. (ed.) *Proc. Workshop on Electron Cooling and Related Applications (ECOL84)* (KfK 3846, Karlsruhe, 1985).
- Spitzer, L. *Mon. Not. R. astr. Soc.* **100**, 396-405 (1940).
- Spitzer, L. *Physics of Fully Ionized Gases* (Interscience Publishers, New York, 1956).
- Habfast, C. *et al. Phys. Scripta* **T22**, 277-281 (1988).
- Poth, H. *et al. Proc. 4th Workshop on Physics at LEAR with Cooled Low Energy Antiprotons* (eds Amsler, C. *et al.*) 121 (Harwood Academic, Chur, 1988).

- Poth, H. *et al. Z. Phys.* **A332**, 171-188 (1989).
- Wolf, A. *et al. Proc. 1st European Accelerator Physics Conf.* (ed. Tazzari, S.) 205 (World Scientific, Singapore, 1989).
- Parkhomchuk, V. V. & Pestrikov, D. V. *Soviet Phys. Tech. Phys.* **25**, 818-822 (1980).
- Dikansky, N. S. & Pestrikov, D. V. *Proc. workshop on Electron Cooling and Related Applications (ECOL 84)* 275 (KfK 2846, Karlsruhe, 1985).
- Dementev, E. N., Dikansky, N. S., Medvedko, A. S., Parkhomchuk, V. V. & Pestrikov, D. V. *Soviet Phys. Tech. Phys.* **25**, 1001-1003 (1980).
- Parkhomchuk, V. V. *Proc. Workshop on Electron Cooling and Related Applications (ECOL 84)* 71 (KfK 3846, Karlsruhe, 1985).
- Schiffer, J. P. & Kienle, P. *Z. Phys.* **A321**, 181 (1985).
- Rahman, A. & Schiffer, J. P. *Phys. Rev. Lett.* **57**, 1133-1136 (1986).
- Habs, D. *Frontiers of Particle Beams*, (eds Month, M. & Turner, S.) 310 (Springer, Berlin, 1986).
- Hasse, R. W., Hofmann, I. & Liesen, D. (eds) *Proc. Workshop on Crystalline Ion Beams (GSI-Report GSI-89-10)* (GSI, Darmstadt, 1989).
- Dikansky, M. S. *et al. Proc. 1st European Accelerator Physics Conf.* (ed. Tazzari, S.) 529 (World Scientific, Singapore, 1989).
- Bell, M. & Bell, J. S. *Particle Accelerators* **12**, 49-52 (1982).
- Gabrielse, G. *et al. Phys. Rev. Lett.* **63**, 1360-1363 (1989).
- Friesel, D. L. *et al. Nucl. Instrum. Meth.* **B40/41**, 927-933 (1989).
- Pollock, R. E. *IEEE Trans. Nucl. Sci.* **NS-30**, 2056-2060 (1983).
- Jaesckhe, E. *et al. Proc. 1st European Accelerator Physics Conf.* (ed. Tazzari, S.) 365 (World Scientific, Singapore, 1989).
- Eckström, C. *et al. Phys. Scripta* **T22**, 256-268 (1988).
- Stensgard, R. *Phys. Scripta* **T22**, 315-317 (1988).
- Franzke, B. *Nucl. Instrum. Meth.* **B24/25**, 18-25 (1987).
- Noda, A. *et al. IEEE Trans. Nucl. Sci.* **NS-32**, 2684-2688 (1985).
- Herriander, C. J., Bárány, A., Rensfelt, K.-G. & Starker, J. *Phys. Scripta* **T22**, 282-285 (1988).
- Pfister, U. *Proc. 1st European Accelerator Physics Conf.* (ed. Tazzari, S.) 398 (World Scientific, Singapore, 1989).
- Olsen, D. K. *et al. Nucl. Instrum. Meth.* **B24/25**, 26-37 (1987).
- Steffens, E. *et al. Proc. 3rd LEAR Workshop on Physics with Cooled Low-Energy Antiprotons in the ACOI Era* (eds Gastaldi, U., Klapisch, R., Richard, J.-M. & Tran Thanh Van, J.) 245 (Editions Frontieres, Gif-sur-Yvette, 1984).
- Ericson, T. E. O. *Proc. Workshop on Nuclear Physics with Stored, Cooled Beams* (eds Schwandt, P. & Meyer, H. O.) 172 (American Institute of Physics, New York, 1985).
- Kilian, K. *Proc. Workshop on Nuclear Physics with Stored, Cooled Beams* (eds Schwandt, P. & Meyer, H. O.) 319 (American Institute of Physics, New York, 1985).
- Datz, S., Andersen, L. H., Briand, J.-P. & Liesen, D. *Phys. Scripta* **T22**, 224-227 (1988).
- Poth, H. & Wolf, A. *Phys. Lett.* **A94**, 135-138 (1983).
- Poth, H. *Z. Phys.* **A326**, 483-486 (1987).
- Poth, H. & Wolf, A. (eds) *Proc. Symp. on the Production and Investigation of Atomic Antimatter (ANTIMATTER '87)* (Scientific Publishing Company, Basel, 1988).

Calibration of the ^{14}C timescale over the past 30,000 years using mass spectrometric U-Th ages from Barbados corals

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Uranium-thorium ages obtained by mass spectrometry from corals raised off the island of Barbados confirm the high precision of this technique over at least the past 30,000 years. Comparison of the U-Th ages with ^{14}C ages obtained on the Holocene samples shows that the U-Th ages are accurate, because they accord with the dendrochronological

calibration. Before 9,000 yr BP the ^{14}C ages are systematically younger than the U-Th ages, with a maximum difference of $\sim 3,500$ yr at $\sim 20,000$ yr BP. The U-Th technique thus provides a way of calibrating the radiocarbon timescale beyond the range of dendrochronological calibration.

RECENTLY a suite of coral cores has been raised off the island of Barbados, and more than 30 *Acropora palmata* samples were dated by conventional ^{14}C techniques¹. The analyses showed that the last deglaciation started at $\sim 15,000$ ^{14}C yr BP (before present), and that it occurred in two steps—observations in full agreement with ^{18}O records in deep-sea cores dated by accelerator mass spectrometry (AMS) of ^{14}C (refs 2-4). The

Barbados offshore collection of corals is also ideally suited for addressing two important problems: the timing of the last glacial cycle and the calibration of the ^{14}C timescale back to 30 kyr BP.

It is now well documented that radiocarbon dating is not a totally accurate chronometer because the atmospheric $^{14}\text{C}/\text{C}$ reference level has changed with time. The first evidence of a discrepancy between true age and ^{14}C age, $\Delta^{14}\text{C}$, was reported by De Vries⁵, and the most accurate evidence of changes of the $^{14}\text{C}/\text{C}$ ratio in the atmosphere (expressed as ‰ above a modern standard, ref. 6) comes from the dating of tree rings⁷. Over the past 9,000 yr, the $\Delta^{14}\text{C}$ curve is characterized by a long

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decreasing trend with a maximum difference of $\sim 100\%$ at about 7,000 yr BP. This trend has been correlated with changes of the magnetic dipole which acts as a shield to the production of ^{14}C by the cosmic rays. Whether or not this slow change is the result of variations in the ^{14}C -reservoir exchange rate rather than changes of the cosmogenic production is still being debated⁸⁻¹¹. Superimposed on the long trend are oscillations¹²⁻¹⁴, which are attributed to short-term variations of the magnetic properties of the solar wind^{13,14}. Before 9,000 yr BP the ^{14}C timescale is not accurately calibrated because of the lack of suitable fossil trees for dendrochronological dating. Several authors have attempted to extend the calibration using other means of establishing absolute ages: varved sediment^{15,16}, U-Th¹⁷⁻¹⁹ and ice cores²⁰. The results obtained are not very precise and are often in disagreement with one another (up to 1,000%). Nevertheless it seems that before 9,000 yr BP the ^{14}C ages are consistently younger than the true ages, suggesting higher $^{14}\text{C}/\text{C}$ ratios than present (a positive $\Delta^{14}\text{C}$).

Recently ^{234}U - ^{230}Th dating of corals by thermal ionization mass spectrometry (TIMS) has been demonstrated²¹⁻²⁵ to be significantly more precise and accurate than the α -counting method. It has also been predicted that U-Th dating would be even more precise than the ^{14}C in the time range of the last deglaciation (6-20 kyr). We have implemented this technique at the Lamont-Doherty Geological Observatory and measured Th and ^{14}C ages in the same coral samples to enable comparison of the two geochronometers. Here we focus on the U-Th/ ^{14}C comparison for the past 30,000 years. The implications of the data for the timing of the last glacial cycle as well as other U-Th ages obtained on older corals (back to 130,000 yr) will be described elsewhere (E.B., B.H. and R.G.F., manuscript in preparation).

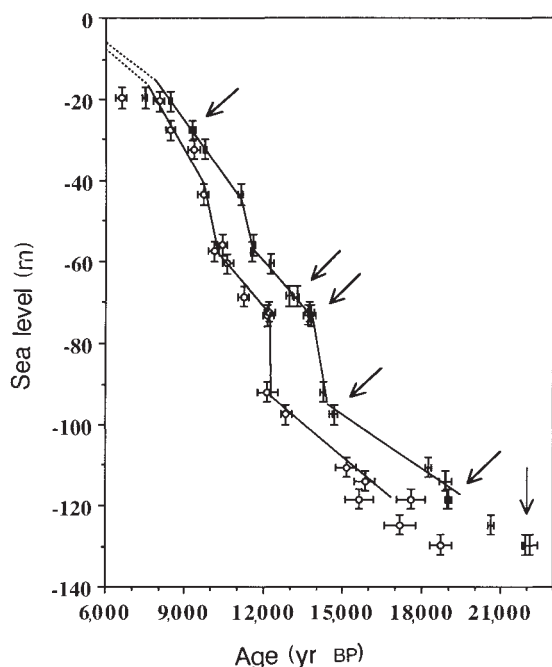


FIG. 1 Sea level during the last deglaciation. Crosses correspond to U-Th ages and the open symbols to ^{14}C ages (calculated with the 5,730-yr half-life). Highest and two lowest samples are composed of *Porites asteroides* and thus only represent lower bound for the sea level at those times. All other samples are *Acropora palmata*. The age errors are quoted at 2σ . The samples marked by arrows correspond to duplicate analyses of the same coral sample by U-Th mass spectrometry. All duplicates are in agreement within the limits of error. A linear uplift correction has been applied by assuming that the last interglacial highstand was at 7 m above the present sea level. This correction is of the order of the inherent error due to *A. palmata* habitat range (± 2.5 m).

Methods

All isotope measurements were performed on a VG Micromass 30, single-collector mass spectrometer, equipped with an analog Daly detector for the analysis of small-abundance isotopes. The techniques used for chemical separation and mass spectrometry of U and Th have been adapted from ref. 22. They will be described in detail elsewhere (E.B., B.H., R.G.F. and A.Z., manuscript in preparation).

For thorium we used a ^{229}Th spike for measurement of ^{230}Th by isotope dilution. The absolute concentration of this spike was calibrated against a dilution of a SPEX ThO_2 standard. For the corals measured so far, the $^{232}\text{Th}/^{230}\text{Th}$ ratios are generally lower than 30 and therefore no correction for detrital ^{230}Th is required because the typical crustal $^{232}\text{Th}/^{230}\text{Th}$ values are of the order of 10^5 (ref. 23). For uranium we used a ^{236}U spike with 99% enrichment for the measurement of ^{238}U and ^{234}U abundances. The absolute concentration of this spike was calibrated against a dilution of NBL CRM111 ^{233}U standard. The accuracy of our correction procedures for isotope fractionation and mass 238 contribution was checked using the NBS U-010 solution: for the $^{234}\text{U}/^{238}\text{U}$ atomic ratio the weighted mean of six measurements is $(5.43 \pm 0.02) \times 10^{-5}$ in agreement with the NBS-certified isotope ratio of $(5.466 \pm 0.06) \times 10^{-5}$.

Results

Table 1 gives the list of U-Th results; as an initial check of the accuracy and precision of our dating technique we dated samples collected from the uplifted reefs of Barbados and Haiti, which correspond to the last interglacial period (samples AFM3, C4 and C1 cf Table 1). These measurements agree with previous α -counting results²⁶ and confirm that Th ages measured in samples from the last interglacial highstand are restricted to the time between 120 and 130 kyr BP (ref. 23).

The precision of the U-Th dating is typically better than 100 yr (at 2σ) for ages between 6 and 20 kyr, significantly better than that achieved for most ^{14}C dating. In addition, replicate analyses of the same hand samples demonstrate that the method is reproducible within the 2σ errors (nine duplicate couples; see Table 1). Initial $^{234}\text{U}/^{238}\text{U}$ ratios calculated using the Th ages fall in the range of modern sea water (1.14-1.15; ref. 21) for all deglaciation samples. This shows that their U-Th systematics have not been strongly altered after deposition.

Figure 1 focuses on the coral record of the last deglaciation dated by U-Th and ^{14}C . The implication of this plot on the chronology and structure of the last deglaciation is described elsewhere (E.B., B.H. and R.G.F., manuscript in preparation). It is remarkable that there is not even a single stratigraphic inversion in the U-Th data. This shows that erosion and redeposition of coral fragments are minor problems in our Barbados core collection.

Samples RGF9-27-5 (dated at Geochron) and RGF9-27-4 (dated at Lamont-Doherty) correspond to the same depth in core 9 (5 cm from each other) but the difference in ^{14}C age (1,900 yr) is very large. The ^{14}C date at 17 kyr BP is considered to be anomalous as it produces a stratigraphic inversion in the core-9 sequence (see Table 1 and ref. 1).

The measurements of ^{14}C in corals cannot be used directly for calibration against absolute chronometers because the surface layer of the ocean is not in equilibrium with the atmosphere; instead, a steady-state balance is maintained between the input of ^{14}C from the atmosphere and its removal by advection and radiodecay in the water column. The ^{14}C ages obtained on corals must therefore be corrected for the age difference between the atmosphere and the surface ocean. This parameter depends mainly on the upwelling and mixing with old sub-surface water masses. For the low-latitude range the reservoir age is generally ~ 400 yr (50%) and is not likely to have changed by more than 100-200 yr during the late Pleistocene²⁷. We have therefore adjusted the raw ^{14}C ages by 400 yr in Fig. 1 and the following discussion.

TABLE 1 U/Th and ^{14}C results from Barbados corals

Sample	Species	Depth (m)	^{238}U (p.p.m.)	$^{230}\text{Th}/^{234}\text{U}$	$^{234}\text{U}/^{238}\text{U}$	$(^{234}\text{U}/^{238}\text{U})_{\text{init}}$	Th age (yr BP)	^{14}C age (yr BP)	$^{14}\text{C}_{5,730}$ (yr BP)	^{14}C lab
RGF7-4-2	Pa	-18	2.65 ± 0.02	0.0667 ± 0.0007	1.1414 ± 0.0065	1.1444 ± 0.0067	$7,460 \pm 80$	$6,400 \pm 200$	6,586	L-DGO
RGF7-5-5	Ap	-19	3.24 ± 0.02	0.0752 ± 0.0004	1.1468 ± 0.0052	1.1504 ± 0.0053	$8,450 \pm 50$	$7,780 \pm 220$	8,006	Geochron
RGF7-12-2#1	Ap	-25	3.16 ± 0.02	0.0823 ± 0.0008	1.1359 ± 0.0079	1.1395 ± 0.0081	$9,280 \pm 100$	$8,200 \pm 200$	8,439	L-DGO
RGF7-12-2#2			3.31 ± 0.02	0.0820 ± 0.0007	1.1455 ± 0.0088	1.1494 ± 0.0091	$9,250 \pm 80$			
RGF7-16-2	Ap	-30	3.19 ± 0.01	0.0861 ± 0.0004	1.1456 ± 0.0040	1.1497 ± 0.0041	$9,730 \pm 50$	$9,050 \pm 250$	9,313	Geochron
RGF7-27-4	Ap	-41	3.45 ± 0.02	0.0975 ± 0.0006	1.1411 ± 0.0061	1.1456 ± 0.0063	$11,090 \pm 70$	$9,400 \pm 200$	9,673	L-DGO
RGF12-5-2	Ap	-53	3.17 ± 0.02	0.1016 ± 0.0005	1.1407 ± 0.0043	1.1454 ± 0.0045	$11,590 \pm 60$	$10,100 \pm 200$	10,394	L-DGO
RGF12-6-7	Ap	-55	3.04 ± 0.02	0.1011 ± 0.0006	1.1463 ± 0.0062	1.1512 ± 0.0064	$11,530 \pm 70$	$9,800 \pm 200$	10,085	L-DGO
RGF12-9-5	Ap	-58	3.04 ± 0.01	0.1072 ± 0.0007	1.1462 ± 0.0056	1.1514 ± 0.0058	$12,260 \pm 90$	$10,300 \pm 200$	10,600	L-DGO
RGF12/16/05#1	Ap	-65	2.96 ± 0.01	0.1151 ± 0.0009	1.1399 ± 0.0048	1.1453 ± 0.0050	$13,220 \pm 110$	$10,900 \pm 200$	11,217	L-DGO
RGF12/16/05#2			3.02 ± 0.01	0.1130 ± 0.0010	1.1402 ± 0.0071	1.1455 ± 0.0074	$12,970 \pm 120$			
RGF12-21-6	Ap	-69	3.03 ± 0.02	0.1190 ± 0.0014	1.1446 ± 0.0064	1.1503 ± 0.0067	$13,700 \pm 170$	$11,850 \pm 200$	12,195	L-DGO
RGF12/21/10#1	Ap	-70	3.33 ± 0.02	0.1198 ± 0.0011	1.1335 ± 0.0057	1.1388 ± 0.0060	$13,800 \pm 140$	$11,800 \pm 200$	12,143	L-DGO
RGF12/21/10#2			3.21 ± 0.02	0.1186 ± 0.0011	1.1395 ± 0.0107	1.1450 ± 0.0112	$13,660 \pm 140$			
RGF9-8-2	Ap	-89	3.06 ± 0.02	0.1233 ± 0.0008	1.1372 ± 0.0069	1.1429 ± 0.0072	$14,230 \pm 100$	$11,800 \pm 400$	12,143	L-DGO
RGF9-13-3#1	Ap	-94	3.22 ± 0.02	0.1267 ± 0.0013	1.1309 ± 0.0058	1.1365 ± 0.0061	$14,660 \pm 160$	$12,500 \pm 200$	12,864	L-DGO
RGF9-13-3#2			3.22 ± 0.02	0.1271 ± 0.0008	1.1314 ± 0.0061	1.1370 ± 0.0064	$14,700 \pm 100$			
RGF9-21-11	Ap	-106	3.52 ± 0.03	0.1552 ± 0.0011	1.1358 ± 0.0039	1.1430 ± 0.0042	$18,240 \pm 140$	$14,700 \pm 400$	15,128	L-DGO
RGF9/24/04	Ap	-109	3.36 ± 0.02	0.1603 ± 0.0019	1.1346 ± 0.0079	1.1420 ± 0.0084	$18,890 \pm 250$	$15,400 \pm 400$	15,848	L-DGO
RGF9-27-5#1	Ap	-114	3.43 ± 0.01	0.1610 ± 0.0007	1.1363 ± 0.0050	1.1439 ± 0.0053	$18,980 \pm 90$	$17,085 \pm 520$	17,582	Geochron
RGF9-27-5#2			3.45 ± 0.02	0.1614 ± 0.0008	1.1391 ± 0.0055	1.1468 ± 0.0058	$19,030 \pm 100$			
RGF9-27-4	Ap	-114						$15,200 \pm 400$	15,642	L-DGO
RGF9-32-4	Pa	-120	3.15 ± 0.02	0.1735 ± 0.0009	1.1329 ± 0.0048	1.1409 ± 0.0051	$20,610 \pm 120$	$16,700 \pm 600$	17,186	L-DGO
RGF9-34-8#1	Pa	-124	3.22 ± 0.01	0.1836 ± 0.0011	1.1335 ± 0.0041	1.1421 ± 0.0044	$21,930 \pm 150$	$18,200 \pm 400$	18,730	L-DGO
RGF9-34-8#2			3.16 ± 0.02	0.1851 ± 0.0019	1.1349 ± 0.0094	1.1437 ± 0.0101	$22,130 \pm 260$			
RGF12-30-2#1	Ap	-78	3.22 ± 0.02	0.2458 ± 0.0016	1.1255 ± 0.0067	1.1368 ± 0.0074	$30,470 \pm 240$	$27,120 \pm 1,520$	27,909	Geochron
RGF12-30-2#2			3.46 ± 0.02	0.2428 ± 0.0014	1.1314 ± 0.0062	1.1431 ± 0.0068	$30,040 \pm 210$			
AFM3#1	Ap	55	3.04 ± 0.02	0.6944 ± 0.0046	1.1077 ± 0.0072	1.1536 ± 0.0110	$125,100 \pm 1,700$			
AFM3#2			3.12 ± 0.01	0.6941 ± 0.0026	1.1065 ± 0.0037	1.1518 ± 0.0057	$125,100 \pm 1,000$			
Haiti C4#1	Ap	52	2.95 ± 0.01	0.6897 ± 0.0043	1.1094 ± 0.0072	1.1553 ± 0.0109	$123,600 \pm 1,600$			
C4#2			2.95 ± 0.01	0.6937 ± 0.0035	1.1071 ± 0.0051	1.1526 ± 0.0078	$124,900 \pm 1,300$			
Haiti C1	Ap	52	3.10 ± 0.01	0.6843 ± 0.0030	1.1070 ± 0.0050	1.1512 ± 0.0075	$121,900 \pm 1,100$			

Depth or altitude of recovery are relative to the present sea level. Ap and Pa refer respectively to *Acropora palmata* and *Porites asteroideus* samples. The measured atomic ratios have been converted to activity ratios by using the same U-Th half-lives used in ref. 22 (all errors are given by 2σ). Labels #1 and #2 correspond to duplicate U/Th analyses. The initial $^{234}\text{U}/^{238}\text{U}$ ratios are obtained by using the Th ages to correct the measured isotope ratios. L-DGO is the Lamont-Doherty Geological Observatory. Note that there is no significant change of uranium concentration between glacial and Holocene samples. The ^{14}C ages correspond to conventional ages (calculated with the 5,568-yr half-life) and ages calculated with the true 5,730-yr half-life. The ^{14}C ages have been corrected for fractionation and a reservoir age of 400 yr (ref. 27).

The most striking result is that the Th ages are consistently older than the ^{14}C ages, with a maximum difference of ~ 3.5 kyr at ~ 20 Th kyr BP (Fig. 2). The difference between the two chronometers is equivalent to a $\Delta^{14}\text{C}$ of ~ 400 – 500% above the present-day reference level for ages between 18 and 22 kyr BP.

Comparison with previous ^{14}C calibration

The three youngest ^{14}C -dated coral samples (RGF7-4-2, RGF7-5-5 and RGF7-12-2, Table 1) from the Barbados collection are in the range of the precise tree-ring calibration. Our U-Th ages for these samples are in agreement with the dendrochronological ages (7,440–7,140, 8,970–8,380 and 9,420–8,970 yr BP are the calibrated ^{14}C dates to be compared with the Th ages of samples RGF7-4-2, RGF7-5-5 and RGF7-12-2, respectively). For the comparison we used the mixed-layer calibration curve of Stuiver *et al.*²⁸ and for the oldest sample, RGF7-12-2, we used unpublished data (M. Stuiver, personal communication). The good agreement between the two independent calibrations is a confirmation of the accuracy of the U-Th chronometer in corals, at least for the Holocene (see refs 22, 24 for the accuracy on very young corals). Before the Holocene, we cannot yet demonstrate that our U-Th ages are true 'calendar' ages, but we will argue below that this is a reasonable assumption.

Based on a comparison between varve counts and ^{14}C dating in Lake of the Clouds¹⁵, the calibration curve was extended to 11 kyr BP. There is also good agreement between the varve estimates and the U-Th/ ^{14}C comparison (Fig. 2).

From 9 to 13 kyr BP, attempts have been made to use the Swedish varve chronology to extend the ^{14}C calibration. These sediments were never directly dated by ^{14}C , however, and the Swedish chronology was tied to the present only recently²⁹. Even in its latest version the $\Delta^{14}\text{C}$ curve based on the Swedish varves correlation is still not in agreement with the Lake of the Clouds record for the interval between 8 and 11 kyr BP and also disagrees with our Barbados results. Stuiver³⁰ concluded that a few hundreds of varves are missing in the Swedish chronology.

At $\sim 10,000$ ^{14}C yr BP (Preboreal/Younger Dryas boundary) the U-Th calibration ($\sim 11,500$ Th yr BP) is in relatively good agreement with the dendrochronological estimates ($\geq 11,300$

dendro yr BP, ref. 31). These two independent estimates are in disagreement with the correlation between climate spectra dated by annual counting of seasonal variations in the ^{18}O content, dust and acidity curves from the Dye III and Camp Century ice cores ($\sim 10,700$ yr BP, ref. 20).

A detailed analysis of the U-Th/ ^{14}C calibration indicates that the true duration of the Younger Dryas climate event (10,000–11,000 ^{14}C yr BP) may have been as long as 1,700 years, in agreement with the qualitative estimates by Oeschger *et al.*³². Moreover, it is not inconsistent with the plateau in ^{14}C ages at $\sim 9,500$ ^{14}C yr BP seen in the dendrochronological data of ref. 31.

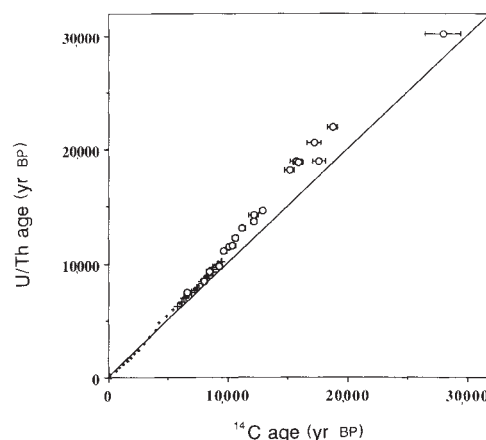


FIG. 2 Open symbols represent the U-Th ages plotted against ^{14}C ages (calculated with the 5,730-yr half-life). The small crosses correspond to the dendrochronological calibration⁷ and the large crosses to the Lake of the Cloud varved sediments¹⁵. For clarity the duplicate analyses by U-Th mass spectrometry have been averaged. The age errors are quoted at 2σ (in the case of U-Th ages they are always smaller than the size of the symbol). For sample RGF9-27-5 we have used the ^{14}C analyses of sample RGF 9-27-5 (Geochron) and RGF9-27-4 (Lamont-Doherty). This study suggests that the ^{14}C age of ~ 17 kyr is anomalous (stratigraphic inversion, see Table 1). For the three younger samples, the good agreement between the tree-ring calibration and our U-Th/ ^{14}C estimates indicate that the Th ages are accurate.

Other attempts of radiocarbon calibration have been made by comparing ^{14}C ages with U-Th ages obtained in samples from dried lakes or speleothems¹⁷⁻¹⁹. For these works the U-Th ages were obtained by α -counting with a much lower precision than by mass spectrometry (the 2σ errors are typically 10-20% of the ages) and a considerable uncertainty is associated with a ^{14}C correction for the initial age of the bicarbonate. Nevertheless, the Barbados U-Th data agree with the study on a south African speleothem¹⁹ and with the Searles Lake record^{17,18} if we use the ^{14}C reservoir age for this lake suggested by Broecker and Kaufman³³.

For the 12,000-25,000 ^{14}C yr BP period other authors have found large discrepancies between ^{14}C and K/Ar dating⁵² and between ^{14}C and thermoluminescence dating⁵³, in agreement with our Barbados results.

Possible geochemical artefacts

One explanation for the increasing lag between ^{14}C and Th ages could be that the samples were contaminated by recent carbon, either *in situ* and/or during the ^{14}C determinations. To correct the ^{14}C ages back to the Th ages, a contamination of ~4% modern carbon is required. We consider that this is highly unlikely because: (1) replicates conducted so far by AMS do not show any significant difference whether or not the coral sample is strongly leached before processing (conducted on samples RGF9-21-11, RGF12-30-2, RGF1-17-4; E.B., M. Arnold, B. H. and R.G.F., manuscript in preparation); (2) the ^{14}C ages obtained by Fairbanks¹ were measured by β -counting in two different laboratories (Lamont-Doherty, without leaching the samples; Geochron lab, with leaching of the samples); and (3) 2% of contamination is the maximum acceptable to keep

the three recent ages in agreement with the tree-ring ages. A definitive test of the accuracy of the ^{14}C ages used in this comparison will be to replicate all the measurements by AMS.

The good quality of the corals for U-Th was tested by X-ray diffraction which showed that no secondary calcite was detectable in the corals. This test is important, but not sufficient, to rule out any diagenetic alteration or uranium exchange³⁴. The strongest argument for the quality of the samples comes from the U-Th measurements themselves: all the initial $^{234}\text{U}/^{238}\text{U}$ ratios fall in the range of the modern sea water (activity ratio between 1.14 and 1.15, ref. 21) in contrast with older air-exposed samples (Table 1, see also ref. 22 and B.H., E.B. and R.G.F., manuscript in preparation).

A gradual loss of uranium could also explain the discrepancy between the two geochronometers. This dissolution can be modelled with first-order kinetics³⁴. A rate of uranium loss equivalent to $k = 7\lambda_{234}$ (where λ_{234} is the decay constant of ^{234}U) would be required to reconcile the ^{14}C ages with the U-Th ages. This explanation seems unlikely, however, because a strong decrease in the uranium concentration with time should be evident in the record (at ~30 kyr BP the decrease should be 50%). The data in Table 1 demonstrate that the uranium concentration in the corals is actually rather constant (3-3.5 p.p.m.), in agreement with other published estimates for *A. palmata*²².

Carbon cycle changes

The ^{14}C -age calculation relies on the assumption that the atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio has not changed with time and therefore can be used to normalize the measured ratio in fossil carbon³⁵. Unfortunately, the atmosphere contains less than a ton of ^{14}C and most of the radiocarbon is in the ocean (>40 tons). Subtle changes in the reservoir sizes and/or rates of exchange between reservoirs could have significantly affected the ^{14}C content of the atmosphere. CO_2 measurements in old polar ice showed that the atmospheric concentration was lower during the last glacial than during the Holocene³⁶⁻³⁸. Box-model calculations show that the steady-state $\Delta^{14}\text{C}$ would be increased by 25-75%

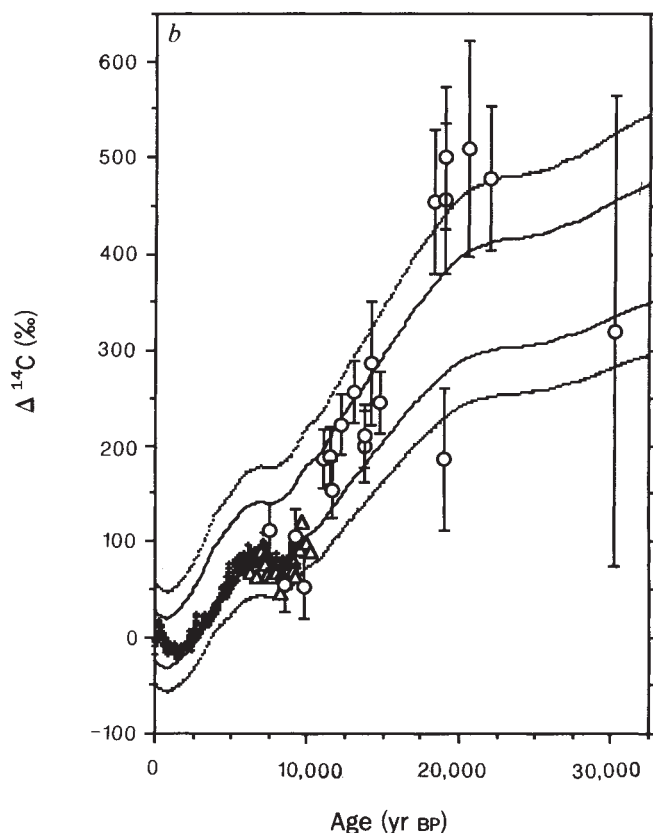
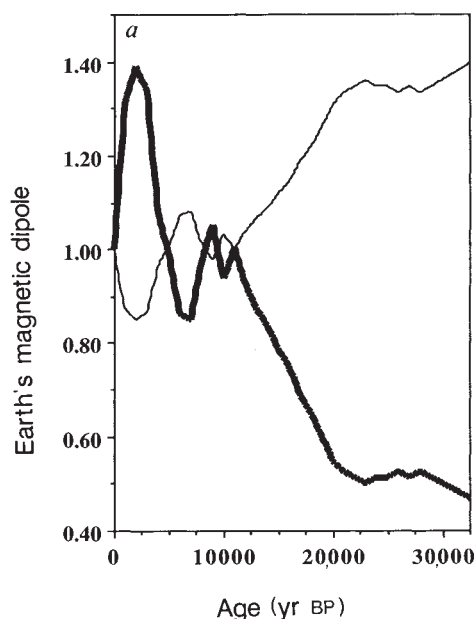


FIG. 3 a, Thick line, intensity of Earth's magnetic dipole reconstructed through time (adapted from ref. 48); thin line, cosmogenic nuclide production through time calculated using these palaeomagnetism data and theoretical calculations by Lal⁵⁰. The scale is normalized to unity for present-day values. Using b, atmospheric $\Delta^{14}\text{C}$ through time reconstructed by the U-Th/ ^{14}C age relationship (open symbols, the errors are quoted at 2σ). The small crosses correspond to the tree-ring calibration⁷ and the open triangles to the Lake of the Cloud calibration (ref. 15, no error has been represented). The two sets of solid lines correspond to the envelopes of $\Delta^{14}\text{C}$ expected as a response to changes of the Earth's magnetic field: for those calculations we have assumed constant errors of ± 5 and $\pm 10\%$ of the present-day dipole. For sample RGF 9-27-5 we have used the ^{14}C analyses of sample RGF9-27-5 (Geochron) and RGF9-27-4 (Lamont-Doherty). This study suggests that the ^{14}C age of ~17 kyr is anomalous (stratigraphic inversion, see Table 1).

depending on the glacial-to-interglacial CO_2 variation and on the version of the box model used^{39–41}.

It is possible to increase further the atmospheric $\Delta^{14}\text{C}$ by diminishing the rate of penetration of $^{14}\text{CO}_2$ in the deep sea. But, to increase the atmospheric $^{14}\text{C}/\text{C}$ by 400% it would be necessary to change dramatically the relative ^{14}C age of the deep waters. By contrast, the mixed layer of the ocean is rapidly exchanging with the atmosphere. A model calculation similar to that of Oeschger *et al.*⁴² shows that the difference in ^{14}C between the surface and the deep sea would have to be increased by ~ 3.5 kyr to account for a 400% higher atmospheric $^{14}\text{C}/\text{C}$ (ref. 27). This age difference is not supported by the palaeoceanographic data on benthic-planktonic pairs of foraminifera dated by ^{14}C AMS. These studies have shown that the ventilation age difference was higher in the Pacific by $\sim 500 \pm 100$ yr (refs 43, 44) and in the Atlantic by 200 ± 200 yr (ref. 44). Assuming that the highest values measured in the Pacific are valid for the global ocean would lead to a maximal atmospheric $^{14}\text{C}/\text{C}$ ratio increase of $\sim 70\%$.

In summary, changes in the carbon cycle can account for only ~ 100 – 150% increase in the $\Delta^{14}\text{C}$ of the atmosphere as compared to the 400–500% inferred from the Barbados data.

Changes in the ^{14}C production

The mean $^{14}\text{C}/\text{C}$ ratio of the exchangeable carbon on the Earth is maintained by a steady state between production by cosmic rays in the upper atmosphere and radiodecay. The $\Delta^{14}\text{C}$ of the atmosphere can therefore undergo variations in response to changes in the flux of galactic protons, solar-wind magnetic properties or the dipole moment of the Earth.

Little is known about possible variations of the cosmic rays on the timescale of interest. As discussed below, the main $\Delta^{14}\text{C}$ variations during the Holocene can be explained by changes of the magnetic field and/or changes in the ocean circulation. Therefore it is not necessary to call for modulation of the galactic protons, and this flux can be assumed to be constant with time until data is produced to the contrary.

Changes in the solar-wind modulation are also poorly known but it is important to mention that Raisbeck *et al.*⁴⁵ have described brief periods of enhanced cosmogenic production during the past 80 kyr, which they attribute to solar effects. Their work, based on AMS measurements of ^{10}Be in the Vostok ice core, shows that the strongest event occurred at ~ 35 and 60 kyr BP. In general, the ^{10}Be record obtained in ice cores shows consistently higher concentrations during glacial stages than during warmer periods (a factor of two for the last deglaciation), but the generally accepted interpretation is that precipitation was strongly reduced during the cold periods⁴⁶. Consequently, aside from the solar ^{10}Be spikes, it is extremely difficult to separate the climate signal and the cosmogenic-production signal embedded in the measurements of ^{10}Be in ice cores.

What is well documented, however, is the fact that the magnetic moment of the Earth has varied significantly over the past several thousand years, as first shown by Thellier and Thellier⁴⁷. The palaeointensity record for the past 40 kyr is characterized by two important features: a quasi-sinusoidal variation during the Holocene and a decrease of the moment by a factor of two before 20 kyr BP (refs 48, 49 and Fig. 3a).

We converted this dipole history into a ^{14}C production time series by using the calculations of Lal (ref. 50; Fig. 3a). The atmospheric ^{14}C production curve cannot be compared directly with the $\Delta^{14}\text{C}$ record, however, because the ^{14}C atoms mix continuously in other carbon reservoirs where they ultimately decay with a mean half-life of 8,270 yr. The carbon cycle therefore has a long 'memory', which can easily be simulated by using a simple box model^{39,51}. The carbon cycle acts as a low-pass filter: short-term production variations (such as the 11-yr solar cycle) are smoothed out and a phase shift of a few kyr is introduced for the transition between the Pleistocene and the Holocene^{39,51}. The results of the calculation are shown in Fig.

3b. We assumed no error on the ^{14}C production algorithm⁵⁰ and constant errors of 5 and 10% of the present-day magnetic field on the palaeomagnetic record. There is clear agreement between the $\Delta^{14}\text{C}$ data calculated from the U-Th/ ^{14}C comparison and our calculation based on the palaeomagnetic record. The $\Delta^{14}\text{C}$ values around 18–22 kyr BP are, however, higher on average than the palaeomagnetism reconstruction, which may indicate that $\sim 100\%$ of the signal is the result of reservoir changes associated with the last glacial maximum.

It must be mentioned that some of the palaeomagnetism data compiled by McElhinny and Senanayake⁴⁸ were dated by ^{14}C . Using our calibration (Fig. 2) to correct the timescale would only stretch the predicted $\Delta^{14}\text{C}$ curve by a few kyr. The U-Th/ ^{14}C would still be well within the errors of the geomagnetic reconstruction of the $\Delta^{14}\text{C}$ curve. Therefore the most reasonable explanation for the large difference between the ^{14}C and U-Th ages involves magnetic modulation of the atmospheric ^{14}C production rate.

Discussion

We have shown here that by using U-Th mass spectrometry one can achieve an age precision and reproducibility comparable to or even better than that obtained by the radiocarbon geochronological method. U-Th ages measured in corals drilled off the shore of Barbados indicate that the ^{14}C timescale is significantly compressed during the late glacial interval. These results can be explained mainly as the consequences of changes in the cosmogenic nuclide production linked to the gradual decrease of Earth's magnetic field⁴⁸. Changes in the carbon cycle^{36–39,43,44} can account for ~ 10 – 20% of the age discrepancy observed between the two geochronometers. It should be borne in mind that the accuracy of the U-Th ages is proven only back to 10,000 years; nevertheless, all geophysical information available (dendrochronology, varve dating and palaeomagnetism) suggests that our U-Th results are reasonable and that they may be used as a first-order tool to calibrate the radiocarbon timescale beyond the range of the high-resolution dendrochronological comparison. □

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1. Fairbanks, R. G. *Nature* **342**, 637–642 (1989).
2. Duplessy, J. C. *et al.* *Nature* **320**, 350–352 (1986).
3. Bard, E. *et al.* *Nature* **328**, 791–794 (1987).
4. Broecker, W. S. *et al.* *Nature* **333**, 156–158 (1988).
5. De Vries, H. L. *Proc. Koninkl. Ned. Akad. Wetenschap.* **B61**, 94–102 (1958).
6. Stuiver, M. & Polach, H. A. *Radiocarbon* **19**, 355–363 (1977).
7. Stuiver, M. & Kra, R. *Radiocarbon* **28**, 805–1030 (1986).
8. Lal, D. *Geophys. Monogr. Ser.* **32**, 221–233 (1985).
9. Beer, J. *et al.* *Nature* **331**, 675–679 (1988).
10. Andree, M. *et al.* *Clim. Dyn.* **1**, 53–62 (1986).
11. Peng, T. H. *Radiocarbon* (in the press).
12. Suess, H. in *Proc. Conf. Problems Related to Interplanetary Matter* NAS-NSF Publ. 845, Nucl. Sci. Ser. Vol. **33**, 90–95 (NAS-NSF, La Jolla, 1961).
13. Stuiver, M. *J. geophys. Res.* **66**, 273–276 (1961).
14. Stuiver, M. & Quay, P. D. *Science* **207**, 11–19 (1980).
15. Stuiver, M. in *Late Cenozoic Glacial Ages* (ed. Turekian, K. K.) 57–70 (Yale Univ. Press, New Haven, 1970).
16. Tauber, H. in *Nobel Symp. 12th, Radiocarbon Variations and Absolute Chronology* (ed. Olsson, I. U.) (Wiley, New York, 1970).
17. Peng, T. H., Goddard, J. G. & Broecker, W. S. *Quat. Res.* **9**, 319–329 (1978).
18. Stuiver, M. *Nature* **273**, 271–274 (1978).
19. Vogel, J. C. *Radiocarbon* **25**, 213–218 (1983).
20. Hammer, C. U., Clausen, H. B. & Tauber, H. *Radiocarbon* **28**, 284–291 (1986).
21. Chen, J. H., Edwards, R. L. & Wasserburg, G. J. *Earth planet. Sci. Lett.* **80**, 241–251 (1986).
22. Edwards, R. L. thesis, California Inst. Technol. (1988).
23. Edwards, R. L., Chen, J. H. & Wasserburg, G. J. *Earth planet. Sci. Lett.* **81**, 175–192 (1987).
24. Edwards, R. L., Taylor, F. W. & Wasserburg, G. J. *Earth planet. Sci. Lett.* **90**, 371–381 (1988).
25. Li, W. X. *et al.* *Nature* **337**, 534–536 (1989).
26. Dodge, R. E., Fairbanks, R. G., Benninger, L. K. & Maurrasse, F. *Science* **219**, 1423–1425 (1983).
27. Bard, E. *Paleoceanography* **3**, 635–645 (1988).
28. Stuiver, M., Pearson, G. W. & Braziunas, T. *Radiocarbon* **28**, 980–1021 (1986).
29. Cato, I. *Boreas* **14**, 117–122 (1985).
30. Stuiver, M., Kromer, B., Becker, B. & Ferguson, C. W. *Radiocarbon* **28**, 969–979 (1986).
31. Becker, B. & Kromer, B. *Radiocarbon* **28**, 961–967 (1986).
32. Oeschger, H. *et al.* *Radiocarbon* **22**, 299–310 (1980).
33. Broecker, W. S. & Kaufman, A. *Geol. Soc. Am. Bull.* **76**, 537–566 (1965).
34. Ku, T. L., Ivanovitch, M. & Luo, S. *Quat. Res.* (in the press).
35. Libby, W. F. *Radiocarbon Dating* (Univ. Chicago Press, 1952).
36. Delmas, R. J., Ascencio, J. M. & Legrand, M. *Nature* **284**, 155–157 (1980).
37. Berner, W., Oeschger, H. & Stauffer, B. *Radiocarbon* **22**, 227–235 (1980).
38. Barnola, J. M., Raynaud, D., Korotkevitch, Y. S. & Lorius, C. *Nature* **329**, 408–414 (1987).

39. Siegenthaler, U., Heimann, M. & Oeschger, H. *Radiocarbon* **22**, 177–191 (1980).
40. Keir, R. S. *Earth planet. Sci. Lett.* **64**, 445–456 (1983).
41. Lal, D. & Revelle, R. *Nature* **308**, 344–346 (1984).
42. Oeschger, H., Siegenthaler, U., Schotterer, U. & Gugelmann, A. *Tellus* **27**, 168–192 (1975).
43. Shackleton, N. J. *et al. Nature* **335**, 708–711 (1988).
44. Broecker, W. S. *et al. Paleoceanography* **3**, 659–669 (1988).
45. Raisbeck, G. M. *et al. Nature* **326**, 273–277 (1987).
46. You, F., Raisbeck, G. M., Bourles, D., Loris, C. & Barkov, N. I. *Nature* **316**, 616–617 (1985).
47. Thellier, E. & Thellier, O. *C. r. hebdom. Seanc. Acad. Sci. Paris* **212**, 281–283 (1941).
48. McElhinny, M. W. & Senanayake, W. E. *J. Geomagn. Geoelec.*, Kyoto **34**, 39–51 (1982).
49. Tauxe, L. & Valet, J. P. *Phys. Earth planet. Inter.* **56**, 59–68 (1989).
50. Lal, D. in *Proc. 45th Conf. Solar-Terrestrial Relationships and the Earth Environment in the Last Millennium*, 216–233 (Soc. Italiana di Fisica, Bologna, 1988).
51. Houtermans, J. C., Suess, H. E. & Oeschger, H. *J. geophys. Res.* **78**, 1897–1908 (1973).
52. Gillot, P. Y. & Cornette, Y. *Chem. Geol.* **59**, 202–222 (1986).
53. Valladas, H. & Valladas, G. *Coll. Int. CNRS, Habitats du Paléolithique Supérieur* (Roanne-Villerey, in the press).

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The identification and suppression of inherited neurodegeneration in *Caenorhabditis elegans*

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The dominant mutation *deg-1(u38)* results in a toxic gene product that leads to the late-onset degeneration of a small number of neurons in the nematode *Caenorhabditis elegans*. Both intragenic and extragenic mutations as well as changes in wild-type gene dosage can delay or block the time of onset of the neuronal deaths. The *deg-1* gene has been cloned and a partial complementary DNA reveals that the gene encodes a novel protein that may act as a membrane receptor. Because the late-onset loss of specific sets of neurons, often as a result of dominant mutations, is characteristic of several human neurodegenerative diseases, the analysis of the *deg-1* gene and its suppressors may provide a means of understanding the mechanisms underlying some of these human diseases.

THE selective degeneration of specific classes of nerve cells is characteristic of many inherited human disorders¹ such as Huntington's disease^{2,3}, familial amyotrophic lateral sclerosis⁴, familial Alzheimer's disease⁵ and several cerebellar ataxias⁶. Many of these diseases are caused by dominant alleles that result in late-onset degeneration of the affected nerve cells, but their molecular bases are not known. Insights into how genetic lesions can lead to neuronal degeneration could be obtained by studying animal models with similar defects.

We have characterized a dominant mutation (*u38*) of the *C. elegans* gene *deg-1* (degeneration), that results in the degeneration of a small set of neurons. One striking feature of some of these deaths is that they have a late onset, occurring long after the neurons form synapses and become functional. The *deg-1(u38)* mutation results in an abnormal, toxic form of a gene product that is normally non-essential for neuron viability and function. The affected cells swell to many cell diameters and lyse. Because the *deg-1* gene seems to encode a membrane component, cell lysis may result from compromised membrane integrity. The time of the neuronal degeneration depends upon the level of *deg-1(u38)* mutant gene activity, suggesting that the level of accumulation of toxic product, rather than the time of its initial expression, causes the deaths. Mutations in the *mec-6* gene suppress the *deg-1(u38)* neurodegeneration, as well as

similar neuronal deaths produced by abnormal toxic forms of the *mec-4* gene product. An understanding of how the mutant *deg-1* and *mec-4* gene products result in neurodegeneration, and of how normal *mec-6* (mechanosensory) activity is required for this degeneration might help in the development of methods for preventing or curing neurodegenerative disorders in humans.

The *deg-1(u38)* phenotype

The *deg-1(u38)* mutant was identified in a screen for touch-insensitive mutants following ethyl methanesulphonate (EMS) mutagenesis at 25 °C (ref. 7). The gene is located on the X chromosome (see legend to Fig. 1). The *deg-1(u38)* animals differ from other touch-insensitive mutants^{7,8} in that although both types of mutants are insensitive to the gentle touch of a hair, only the *deg-1* mutants are insensitive to the more severe prod of a thin wire. They are also insensitive only at the tail. This more severe phenotype (designated Tab for Touch abnormal) suggests a defect in the two PVC interneurons, which receive synaptic inputs from posterior touch receptor neurons⁹. The PVC cells degenerate in these mutants. A similar behavioural abnormality results from laser ablation of the PVC cells in wild-type animals (W. W. Walthall and M.C., unpublished data).

Although the PVC cells arise during embryogenesis¹⁰, *deg-1* mutants are touch-sensitive at hatching and become Tab later, during the second and third larval stages (L2 and L3) at 25 °C (Fig. 1). The stage of onset of touch insensitivity is delayed further when animals are grown at lower temperatures, so mutants grown at 15 °C become Tab as gravid adults.

Virtually all *deg-1* animals, when viewed by Nomarski microscopy¹¹, have one or two degenerating cells near the normal position of the PVC cells, 24 h after hatching at 25 °C (Fig. 2). The degeneration is first seen as a small vacuole that surrounds the nucleus. This vacuole, which contains particles displaying Brownian motion, enlarges by several cell diameters over the next few hours, during which the nucleus disintegrates.

This degeneration differs from programmed cell death, a common feature in *C. elegans* development, in which affected cells become refractile and condensed as they die¹¹. Here we use the term degeneration for the type of death seen in *deg-1(u38)* mutants to distinguish it from the morphologically distinct programmed cell death. The *deg-1(u38)* degeneration phenotype (termed Deg) has been seen in animals with dominant mutations of the gene *mec-4* (*mec-4(d)*). Dominant, but not recessive, *mec-4* mutations result in the degeneration of the touch receptor neurons^{7,8}, probably by the production of a toxic product that is expressed within the touch receptor neurons¹². As in *deg-1(u38)* animals, some of the affected cells in *mec-4(d)* mutants display a late-onset degeneration^{8,13}.

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